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AN ECOLOGICAL ASPECT OF THE CONCEPTION OF SPECIES

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In the discussion of this question I do not feel myself hedged in by any limitations, since no one pretends to say what are the bounds of ecology. Indeed, to define a species may be regarded as an easy task, compared with the task of one who sets out to define ecology. And so this occasion affords me a pleasant opportunity to present some views for which I have long desired an audience like this.

It is coming to be realized that the problems of physiology and ecology are essentially identical, not alone in the matter of the species concept, but in all respects. Physiologists and ecologists have come to feel that the experimental method furnishes the only adequate test for determining the validity of species. The method of approach has differed with the point of view, and it is the physiologist who has given most emphasis to the fundamental importance of experimentation. The ecologist, on the other hand, has brought in the rich contributions of field observation. It is only recently that each has recognized the imperative necessity of the method of the other, and it now seems possible to predict that the fundamental method of the future is to be field experimentation combined with observation. No one realizes so well as does the ecologist the inadequacy of laboratory experimentation in the settlement of field problems. The ecologist feels that the species problem is essentially a field problem, and hence incapable of final settlement, either in the herbarium or in the laboratory. Yet it is the exact methods of the laboratory carried into the field that give promise of the solution of the problem of species.

Perhaps no phenomena bring the principles just enunciated into more clear relief than do those of natural selection. Many species must be born that never have an opportunity to survive, owing to their lack of adaptation to the surroundings in which they originate. The mutants of *Œnothera lamarckiana,* though developed under essentially similar conditions, do not appear equally adapted to the environment in which they first appeared; had they been left to themselves, some mutants would have perished, while others (and perhaps especially *Œnothera gigas*) might have lived. The citrus hybrids, developed in government experiments in Florida, form another group of new forms, some of which are best adapted to one climate, and others to another. Since, therefore, no necessary adaptive relation must exist between a new species and the region of its birth, it is clear that the laws of selection determine the success or failure of new species. The interpretation of selection is a field problem, an ecological problem. A theoretical plant species may be produced in the laboratory, but the real species that make up the vegetation of the world are developed and must be studied out of doors.

One of the noblest aims of ecology is the destruction of many of the "species" of our manuals. Where the critical study of species is confined to the herbarium, it often happens that ecological varieties or habitat forms are given specific rank. An excellent instance of this is seen in the case of *Polygonum amphibium* and *P. hartwrightii.* The latter, which looks wonderfully different from the former in herbaria, can be developed at will by growing *P. amphibium* on land instead of in the water. Not infrequently a plant may be found on the edge of a pond, showing branches in the water that would commonly be referred to *P. amphibium,* and aerial branches that would be regarded as *P. hartwrightii.* Bonnier's classic experiments, whereby many alpine plants were shown to be capable of being developed into well-known lowland species in a single generation, illustrate a phenomenon similar to that exhibited by Polygonum. It is likely that our manuals contain many so-called species, such as these, which await reference to ecological varieties.

Having eliminated habitat forms from the rank of species, and having disposed of the influence of natural selection as a destroyer of many incipient species, it remains to discuss the varied ideas concerning the real or supposed species that remain. In the main it may be said that there are two opposing conceptions of species that are to-day struggling for mastery in the realm of biologic thought. The more prevalent idea, dating in its essence from the time of Darwin, has been that species are artificial creations, mere matters of convenience in the classification of the organic world, arbitrary concepts that have no great and enduring reality. Partisans of this view hold to the doctrine of continuity, maintaining that all species have been connected with other species by a series of intergrades, and that there is no vital distinction between variation and mutation. If, indeed, many species, such as the sassafras, differ widely from all other known species, this is because of the elimination of intergrading forms. In the case of Sassafras, this idea is strengthened by the evidence furnished by fossil forms. In somewhat striking contrast to this concept of species stands the idea that species are entities, which arise by discontinuous variation or mutation, and which have their full specific value from the start. Nor does time change specific form by any slow gradations; the species at its death shows no essential difference from the species at its birth. In many instances, at least, these species are of lower rank than the Linnean species, and have been known as small or elementary species. As a rule those who hold to the latter species conception are more prone to appeal to hidden "internal" causes in explaining the origin of new species, while environmental factors in evolution are more commonly held as dominant by those who regard species as indefinite things gradually evolved from other species. In this connection it is curious to note that the idea of a species as an entity, now held by most mutationists, has much in common with pre-Darwinian notions of special creation; it seems to be in part a return to former conceptions of a rigid nature. On the other hand a new idea of species content is set up. Both pre-Darwinians and Darwinians agreed that *Draba verna* is a species, but the new school would maintain that under this name are masquerading a hundred odd real species.

There are, then, two radically different conceptions of species now current, one of a rank as much higher than the other as the genus is above the Linnean species, or the family above the genus. Ecological observations support both views, but it is especially the experimental method that has made things clear. Whether or not one calls them species, it is evident that the genus Œnothera contains a number of entities, sharply defined from one another. In such genera as Salix and Aster there is reason to believe that species do not thus differ sharply, but that they are connected with one another by all but imperceptible gradations; at any rate this condition exists in Leptinotarsa, as conclusively shown by Tower. It seems impossible to homologize species in Œnothera and Leptinotarsa. It appears that the method of evolution in various groups of plants and animals is radically different, and it follows as a corollary that what are called species in these various groups are necessarily not homologous.

In the light of these views the task of the taxonomist is seen to be most difficult; for the convenience of biologists, he must reduce to common terms things that are unrelated; he must homologize things that are not homologous. In such a dilemma there seem two courses open: (1) The Linnean species concept, that has ruled both before and after evolution was accepted by biologists, may be abandoned. The elementary species then becomes the species of taxonomy. Something akin to this has already taken place in certain genera, notably Cratægus, Viola and Sisyrinchium. Those who take this attitude should abandon the year 1753 as a starting point for specific nomenclature, since a new conception of species demands a new datum line. Possibly this datum line is furnished by the experimental work of Jordan on *Draba verna*. Such a revolution would of course be appalling in its consequences. The present status of Cratægus, perhaps, gives an index of what is to come, if this idea is accepted; where now we have dozens of species, we may expect hundreds or even thousands. We may even expect the appearance of a taxonomic daily newspaper with its hourly record of new species and their fluctuations, comparable with market quotations in a period of financial panic. (2) The alternative is to retain the Linnean species concept as a working theory, employing trinomials for elementary species. Thus we should speak of *Œnothera lamarckiana rubrinervis, O. lamarckiana gigas,* etc. One great advantage of following this method would be that we should secure all the advantages of the newer critical study of such genera as Cratægus and Sisyrinchium, and at the same time tie the new work to the old in such a way that those not taxonomists could appreciate the general significance of the results. Very few except Cratægus specialists could tell offhand anything about *Cratægus ellwangeriana* or *C. champlainensis,* but if these forms were denominated respectively, *C. mollis ellwangeriana,* and *C. mollis champlainensis,* many would know their general affinities, In the case of intergrading species without well-defined specific boundaries, the only course is to retain the trinomial for varieties, much as has been done in the past. If it is wished to distinguish between varieties and elementary species, the expression var. might precede the varietal name, as is the custom now with many.

It is to be hoped that the taxonomists, and particularly those taxonomists who have sinned in the much making of species and those who have made a so-called critical study of plants without any adequate training in the general principles of botany, will reform their ways. In truth, they must reform. No longer may each man be a law unto himself. Nor is it right that any group or coterie should make rules and regulations that run counter to the expressed opinions of a world botanical congress. It is doubtful if any single botanist agrees with all of the taxonomic expressions of the Vienna Congress; it is even possible that some agree with none of its provisions. However, it registers a general consensus of opinion, agreed upon by those who thought the congress far too radical, and by those who thought it far too conservative. It marks a step in the taxonomic progress of the botanical world, and there is no surer way to lead toward further progress than in abiding by its provisions; on the other hand, there is no surer way of ensuring the continuation of the taxonomic chaos, of which we have had far too much, than in setting up individual or even provincial or national codes in opposition to a world code. An American school of taxonomy is an anomaly, since many species are world-wide, and should have world-wide names; even the local species should be delimited in accordance with international rules.

Taxonomy must be scientific. It must require for its devotees a training as rigid as that required by professional workers in morphology, physiology or ecology. Species-making by taxonomic tyros must be abandoned. The requirement of Latin diagnoses, though regretted by many of us, may be of help in checking the voluminous contributions of amateurs. In the future it must be recognized that the final test of the validity of species is experimental, and taxonomists must work no less in the herbarium, but more in the field and in the garden. If the taxonomists of the future fail in these respects, a hard but certain fate awaits them. The world of morphologists, physiologists and ecologists has borne with them patiently and long, and has deferentially abided by the specific determinations of the taxonomists. The recent ebullitions of the taxonomic radicals have evoked in botanists in general successively dissatisfaction, contempt and rage. These things will not be endured much longer; a little more and the sinning taxonomists will be "cast out into the outer darkness where there shall be wailing and gnashing of teeth."